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BULLETIN

OF THE

TORREY BOTANICAL CLUB

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CONTENTS

Cell-division of the pollen-mother-cell of Cobaea scandens alba. (Plate 14.) WANDA KIRKBRIDE FARR 325

Apogamy in Osmunda cinnamomea and O. Claytoniana ELIZABETH DOROTHY WUIST BROWN 339

Regeneration in Sphaerocarpos Donnellii . . . . . H. W. RICKETT 347

A misconception as to the structure of the ear of maize PAUL WEATHERWAX 359

INDEX TO AMERICAN BOTANICAL LITERATURE 363

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BULLETIN

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TORREY BOTANICAL CLUB

AUGUST, 1920

Cell-division of the pollen-mother-cell of Cobaea scandens alba

WANDA KIRKBRIDE FARR

(WITH PLATE 14)

Spindle formation in the pollen-mother-cells of *Cobaea scandens* Cav. was studied by Lawson* in 1898. The stages represented in his plates extend from the resting pollen-mother-cell to the time of nuclear reorganization after the second division. With reference to the division of the cell the following statements are made (pp. 177 and 178):

> There is no cell-plate formed until after the second division. . . . In fig. 24 we see three daughter-nuclei in the same plane. By means of the continuous fibers and mantle-fibers they are connected with one another. These fibers now occupy almost the entire cell-cavity. Cell-plates are now formed in the usual way. Swellings appear on the connecting fibers; these increase in size, and finally result in forming cell-walls which separate the daughter-cells from one another.

A complete disappearance of the spindle-fibers is shown to take place (*f. 21, 22*) before the beginning of the second division. The four nuclei resulting from the second division are arranged tetrahedrally in the mother-cell. Every one of the twenty-four cells figured shows evidence of a thickening of the mother-wall.

The behavior of the cells in *Cobaea*, as reported by Lawson, resembles in some respects that of the pollen-mother-cells of *Nicotiana Tabacum*, *Primula sinensis*, *Tropaeolum majus*, and certain other dicotyledons in which cell-division was found by C. H. Farr† to be accomplished, not by the formation of a cell-plate,

[The BULLETIN for July (47: 279–324. *pl. 10–13*) was issued August 9, 1920]

* Lawson, A. A. Some observations on the development of the karyokinetic spindle in the pollen-mother-cells of *Cobaea scandens* Cav. Proc. California Acad. Sci. Bot. III. 1: 168–188. *pl. 33–36*. 1898.

† Farr, C. H. Cytokinesis of the pollen-mother-cells of certain dicotyledons. Mem. N. Y. Bot. Gard. 6: 253–317. *pl. 27–29*. 1916.

but by a process which "involves the furrowing of the protoplast in the plane midway between the nuclei."

The reports of earlier investigators indicated that the majority of dicotyledons formed their microspores by quadripartition. Concerning the details of the process the literature is somewhat inconsistent, as the following summary indicates:

Juel (1900) in the study of *Syringa;* Tischler (1906) in *Ribes, Bryonia, Mirabilis,* and *Potentilla;* and Duggar (1899) in *Bignonia,* stated definitely that cell-plates were formed, but they furnished no details of the process and no figures to illustrate it.

Baranetsky (1880) in his study of *Lathyrus, Hesperis,* and *Ipomoea,* was unable to find cell-plates. His figures show an incipient furrowing of the protoplasts, but he made no comment upon this fact.

Rosanoff (1865) in *Acacia;* Ishikawa (1911) in *Dahlia;* Osawa (1913) in *Taraxacum;* Miss Pace (1912) in *Parnassia;* Shoemaker (1905) in *Hamamelis;* Miss Fraser (1914) in *Vicia;* and Beer (1912) in *Crepis,* indicated in their drawings the absence of cell-plates during cell-division. These authors do not discuss the possibility of cell-division by any other process.

Pringsheim (1859) in the study of *Dahlia;* Rosenberg (1907) in *Hieracium;* and Guignard (1897) in *Magnolia,* likened these forms, in their method of division, to other forms in which the process involved had not been clearly established.

Miss Digby (1912) in the study of *Primula,* and Cannon (1903) in cotton, discussed and figured the constriction of the pollen-mother-cells but failed to state whether or not cell-plates were formed.

A difference of opinion arose concerning the process of division in the pollen-mother-cells of *Althaea.* Wimmel (1850) reported cell-plates; von Mohl (1853), a combination of cell-plates and furrowing; and Pringsheim (1854) reported furrowing. The assertions again lack the necessary background of detail.

Gates (1907) showed a cell-plate in a diagram of a pollen-mother-cell of *Oenothera.* It is accompanied by no explanation of the process.

Naegeli (1842) in *Oenothera, Bryonia,* and *Cucurbita Pepo;* Sachs (1872) in *Tropaeolum;* Strasburger (1873) in *Tropaeolum;*

Lawson (1898) in *Cobaea;* Tischler (1906) in *Bryonia* and *Ribes;* the same author (1908) in *Podophyllum;* and Johnson* (1914) in *Peperomia,* indicated by their figures a type of division differing from that in which cell-plates are formed. In every instance, however, the statement was made that cell-plates were formed.

Miss Nichols (1908) in her study of *Sarracenia* reported a process of division by constriction of the protoplast, but gave no figures to support the idea.

Andrews (1901) reported a combination of cell-plates and furrowing in the division of the pollen-mother-cells of *Magnolia.* No details of the process were discussed.

The early studies of Wimmel (1850) upon *Althaea* and of Hofmeister (1867) upon *Passiflora* indicate, in the light of the recent study by C. H. Farr, a grasp of the essentials of the furrowing process. Perhaps the lack of detail in their presentations, followed by the launching of the more carefully established cell-plate theory, accounted for the lack of recognition of furrowing as a distinct type of pollen-mother-cell division. Special mention is also due Cannon and Miss Digby, who discussed and figured constriction furrows but failed to report the absence of cell-plates; to say nothing of the large group of investigators whose figures indicate the absence of a cell-plate, but who do not commit themselves concerning the nature of the division.

Such fragmentary and contradictory evidence, however, had resulted in leaving the general impression that quadripartition in dicotyledons was accompanied by the formation of cell-plates. It remained for the presentation of a more complete series of stages from the dividing pollen-mother-cells of *Nicotiana Tabacum,* as presented in C. H. Farr's paper, to clearly establish the process of quadripartition by furrowing. It is there shown that the nuclei of the pollen-mother-cells enlarge during pre-synapsis and synapsis; that a thickening of the mother wall also begins during synapsis and continues throughout the nuclear divisions; and that no cytoplasmic division occurs after the first nuclear division. During the metaphases of the homoeotypic division the remaining

* Johnson, D. S. Studies of the development of the Piperaceae,—II. The structure and development of *Peperomia hispidula.* Amer. Jour. Bot. 1: 323–339. *pl. 36–38.* 1914. Other references to the papers here cited are given by C. H. Farr.

spindle-fibers of the first division entirely disappear. After the four nuclei resulting from the second division have been fully reorganized, they assume a tetrahedral arrangement in the cell, and a spindle is formed between every two nuclei, making a total of six spindles. "These spindles," as Farr states, "are indistinguishable from each other, in other words it is not possible to tell, either from the nuclei or from the spindles, which of the four nuclei are sister nuclei." A migration of the nuclei occurs resulting in their appression to the plasma-membrane. The cell cavity then becomes lobed. This, it is further shown, appears to be "due to furrowing of the plasma-membrane along the plane midway between each pair of nuclei. The first indication of the furrowing is to be found in the flattening of the protoplast on four sides, each of which is parallel to the plane of three nuclei, so that the entire protoplast assumes the form of a tetrahedron, the nuclei lying near the corners." The furrowing of the plasma-membrane and the invagination of the mother wall take place simultaneously. The furrowing, however, progresses more rapidly at some places than at others. C. H. Farr's description continues as follows:

> It is evident that if there are four nuclei arranged tetrahedrally and equidistant from each other within a sphere, there will be four points upon the surface of that sphere which are equidistant from each of three of the nuclei. . . . By the transformation of the sphere into a tetrahedron the plasma-membrane has been brought closer to the nuclear-membrane. At these four points above mentioned, on the plasma-membrane, the constriction of the mother-cell continues to proceed more rapidly than elsewhere. . . . These projections, or invaginations, continue to elongate toward the center of the cell, and consequently in the direction of the fourth nucleus, keeping at all times equidistant from the three nuclei. As a result the four projections meet in the center of the tetranucleate cell, and fusion of their tips occurs. . . . Thus there are organized four protoplasmic masses each with a single nucleus and connected with each of the other four by an isthmus of cytoplasm, at first quite broad. . . . Apparently each isthmus constricts independently of the others. . . . Upon the completion of the division each of the four cells is separated from the other three by a lateral wall which is thicker in its periphery and thinner at its center.

The figures of *Cobaea scandens*, drawn by Lawson, show the absence of division of the cell after the first nuclear division; the disappearance of the spindle of the first division before the beginning of the second division; the thickening of the cell wall; the tetrahedral arrangement of the four nuclei; and a furrow-like indentation of the plasma-membrane. These characteristics suggest a type of cytokinesis similar to that of *Nicotiana*. The

plant at least presents for study an instance of quadripartition with no conclusive evidence concerning the presence or absence of a cell-plate during the process of division.

MATERIAL AND METHODS

The material for study was collected from plants of *Cobaea scandens alba* growing in the greenhouse of Columbia University. The large size of the pollen-mother-cells made it possible to determine the stages of their development in the fresh mounts. Upon examination it was found that the cells in all of the anthers of the same bud were in approximately the same stage of development. The material for fixation was then selected by examining one anther from the bud and fixing the four remaining anthers of those which were found to be in the desired stages.

Flemming's strong chromic-acetic-osmic fixing solution was used in the preparation of the material. The sections were made 3–5 μ in thickness, and were stained with Flemming's triple stain.

OBSERVATIONS

The mother-cell at the close of the second nuclear division is very nearly spherical in form. The four nuclei are arranged at this stage and through all of the succeeding stages of microspore formation in a tetrahedral manner within the cell. They are ellipsoidal in form. Their diameter immediately after reorganization is about one-seventh of the diameter of the mother-cell, or 6 μ. An enlargement of the nucleus also takes place during the division of the cell, which results in a diameter of about one-fifth of the mother-cell, or 8.4 μ. The chromatin is at first appressed to the nuclear membrane (FIG. 1.). During the later stages of cell-division it is found scattered throughout the nucleus (FIGS. 3, 4, 7). The nuclei contain one or more larger and several smaller nucleoli, which are usually spherical. Occasionally an oval one may be found among the larger nucleoli. In some sections they are seen to be appressed to the nuclear-membrane (FIGS. 1, 2).

The spindles, of which there are six, a spindle connecting every nucleus with every other one, appear to be inflated (FIG. 1). Spindle-fibers may be found to run along apparently the entire distance from one nucleus to another, and they are quite uniform

in thickness throughout their length. Continuous fibers at the extreme outer portion of the spindle may sometimes be found appressed to the plasma-membrane at about their middle points. In the center of the cell the outer fibers of the spindles are seen to cross one another, and leave no inter-spindle areas except a small, usually triangular space at the center of the cell, due to the curvature of the fibers (FIG. 1).

The spindle-fibers in the *Cobaea* exhibit a very different behavior during cell-division than do the spindle-fibers of the larch and onion, as shown by Timberlake.* In the pollen-mother-cells of the larch and in the vegetative cells of the onion, whose divisions are accompanied by the formation of a cell-plate, the continuous fibers, after nuclear division, show a thickening at their ends near the nuclei. This apparently marks the beginning of the activity of the fiber, which soon develops a very marked thickening in the equator. These enlargements upon the fibers seem to unite and form a layer throughout the thickness of the original spindle. This is accompanied by a shortening of the fibers. The central fibers then continue to shorten until they finally disappear, having been used up in the formaton of the cell-plate. While these activities of the fibers are going on, there appears, in the onion, a zone of orange-staining material, presumably carbohydrate in nature, the probable function of which is to serve as reserve material for cell-wall formation.

The continuous fibers in *Cobaea*, in some cases, show a certain amount of thickening throughout about two-thirds of their length, but they remain attenuated at their ends (FIGS. 2, 7). Occasionally a fiber may be found to be thickened apparently throughout its length (FIGS. 5, 7, 8). This thickening, however, is almost negligible when compared with that found in cell-plate formation. In no instances were there found, in any spindle-fibers of the *Cobaea*, such localized enlargements as those shown by Timberlake and others to precede the formation of a cell-plate. No shortening or disappearance of the fibers in any other manner could be found. The continuous fibers between the nuclei are apparently unchanged during the succeeding stages of cell-division (FIGS. 2–7). They

* Timberlake, H. G. The development and function of the cell plate in higher plants. Bot. Gaz. **30**: 73–99, 154–170. *pl. 8, 9.* 1900.

seem to be some of the last structures in the cytoplasm to be severed before the separation of the daughter-cells (FIGS. 6, 7). Even after this separation finally occurs the halves of these fibers are found to extend from the nuclei to the plasma-membranes of the two microspores separated by the furrows. The behavior of the fibers in connection with the formation of the cell-plate led Timberlake to say, "the whole process seems to indicate a somewhat plastic character of the fiber." The behavior of the fibers of *Cobaea*, as shown by the present study, suggests that such a statement would not apply to them, but that they are more permanent in nature.

Across the equators of the spindles a less dense region of cytoplasm appears at about the time of thickening of the fibers (FIG. 2). This also is evident during the remaining stages of division (FIGS. 3–7). It is apparently made more conspicuous by a denser area around the nuclei, which does not extend into the equatorial regions. The peripheral cytoplasm is fibrillar in nature. The fibrillae show at first no tendency to radiate from the nuclei (FIG. 1). The beginning of such a radiation can be seen in FIG. 2. This continues until a distinct radiation is found in the stage represented by FIG. 4, and the condition is maintained throughout the succeeding stages of division. Scattered irregularly through the cytoplasm are many spherical, red-stained bodies which vary greatly in size. In FIG. 3 five such bodies are shown, which appear to be arranged along a fiber, but in general they have no definite arrangement with reference to any other structures in the cell.

Very soon after the completion of the second nuclear division the cell-wall becomes thickened to about one-fifteenth of the diameter of the mother-cell. This thickening is approximately uniform over the entire surface of most of the cells examined. The loose arrangement of the cells in the pollen-chamber may account for this uniform enlargement. The intercellular spaces are usually large enough to prevent the touching of the different cells. Occasionally they may be found in groups of two or three with the walls of the different cells appressed. At this early stage in division the cell-wall has reached almost its maximum thickness. Cells were rarely found whose wall-thickness exceeded one-fourteenth to one-thirteenth of the diameter of the mother-cell.

After the completion of the second nuclear division, the most striking change in the pollen-mother-cell is its lobed appearance. Upon the plasma-membrane, midway between the polar regions of the three nuclei, there appear sharp indentations pointing toward the center of the cell. In a section, three of these may be in view. FIG. 2 clearly shows two such indentations. The absence of the third one is due to the plane in which the section is cut. The view of the adjoining spindle shows that it is not a median section, such as we have in the two other spindles. The cell-wall conforms to these indentations and the fibers through which the furrows pass, aside from being separated in the center, are apparently undisturbed by it.

During the succeeding stages of division there appear in some of the sections, first at the periphery of the spindle equators, later at different points in the equators, small masses of material which vary in their staining reactions according to their size. The smaller ones stain very darkly, almost black, with gentian violet (FIG. 3). The larger ones stain the same as the cell-wall, with a narrow, dark-stained layer of material upon the outside, apparently a membrane (FIG. 7). These bodies do not appear in all of the sections, but they occur in short rows directly in front of the furrow tips, as shown before one furrow in FIG. 5. They are not seen at this time either along the centers of the spindles or in the center of the cell. If any such bodies were present, beyond these short rows, they would be clearly visible because of the regions of less dense cytoplasm across the equators of the spindles.

A careful examination of the sections in which these masses of material appear has resulted in the conclusion that they are never upon the spindle-fibers, but that they are between them; and that the spindle-fibers have no direct relation to their formation. They are believed to be sections of the furrows which are cutting into the cytoplasm of the pollen-mother-cell. In a section such as that shown in FIG. 3, for instance, there has been cut a portion from one of the faces of the tetrahedral mother-cell, and in it are median sections of three nuclei. If in the unsectioned mother-cell every one of the spindles is cut by a furrow, it can be seen that in cutting off this portion from the mother-cell, three half-furrows have been removed. If this severed portion is viewed upon the

side opposite to the cut surface, there are seen the three lobes of the mother-cell and the three half-furrows meeting at a point equidistant from the centers of the three lobes. These furrows are cutting sharply into the cytoplasm. It has been stated before that the equatorial regions through which these furrows are advancing are composed of very clear cytoplasm. There are then no visible structures in the line of advance of the furrows except the spindle-fibers. An examination of the cut surface of the section will show that the furrows work in between the fibers in their paths, and later surround them. A cross-section of such a furrow would present a wavy appearance upon its advancing edge. The masses of material which appear in the equatorial regions, as shown in FIGS. 3, 5 and 7, are the severed portions of this edge. The smaller portions consist of the plasma-membrane, while the larger portions are of wall material surrounded by plasma-membrane. It may also be observed that these penetrating tips appear first at the peripheral regions of the equators of the spindles. This is what might be expected if the furrow advances uniformly throughout its length.

C. H. Farr found in *Nicotiana* that the furrows advance much more rapidly than elsewhere from the points of intersection of the six furrows. As he states,

> It is thus apparent that these four projections finally meet in the center of the tetranucleate cell, before the furrows have completed the division on the equator of each spindle. . . . . The first indication of the growth of thes eprojections toward the center of the cell is in the straightening of the spindle-fibers. . . . . This straightening results in the fibers pulling away from the center of the mother-cell, leaving a space which is triangular in section, but is really pyramidal, in the center of the cell.

The projections in his plant are also triangular in section and, in his *f. 32*, are shown as they appear during the earlier stages of furrowing.

In the corresponding stages of *Cobaea* no traces of such projections from the intersections of the furrows could be found (FIGS. 3, 4, 5). While in the tobacco the furrows are found to penetrate more deeply at four points, the furrows of *Cobaea* may be conceived of as advancing, in general, more regularly, penetrating only slightly deeper at many points upon their edges. That the appearance of these furrow tips in the sections is due to the planes in which they are cut may be seen from a comparison

of FIGS. 4 and 5. These are adjoining sections of the same pollen-mother-cell. FIG. 4 is drawn from a section cut between FIG. 5 and the fourth nucleus of the cell. Fig. 4 is consequently nearer to the furrows which are advancing from the sides of the lobes, nearer to the fourth nucleus. The projections are very distinct in FIG. 4, but they have not advanced far enough into the cytoplasm to be seen in the section from which FIG. 5 is drawn.

In the center of the cell section, FIG. 6, at the point toward which the tips of the three furrows are pointing, is shown the first appearance of that which will develop, at an even later stage, into the central triangular area of wall material. No straightening of the fibers may be observed to precede it. FIG. 7 represents a very late stage in the process of cell-division, in which the central triangular area may be seen. The furrows have pushed through in other places along the equators of the spindles. Some of the fibers in their paths are not yet surrounded, as can be seen from the drawing. These observations show that except for these slight irregularities the advance of the furrows in *Cobaea* is quite uniform, as has been suggested in connection with their appearance first at the outer portions of the spindle equators. This uniform advance accounts for the appearance of the central triangular section of the furrow at a much later stage than it was found to appear in *Nicotiana*. The daughter cells become almost spherical in form before their complete separation (FIG. 7).

DISCUSSION

The pollen-mother-cells of *Cobaea*, then, present another instance in the microspore formation of dicotyledons, in which the cell-plate is not apparent during cytoplasmic division. The process concerned is, in its general characteristics, like that found by C. H. Farr in *Nicotiana* and other dicotyledons. It differs from *Nicotiana*, however, in possessing some cytoplasmic characteristics similar to those observed in the study of cleavage furrows in the fungi. Mention has already been made of the less dense areas in *Cobaea* which appear across the equators of the spindles during the process of furrowing. Now Harper* found

* Harper, R. A. Cell and nuclear division in *Fuligo varians*. Bot. Gaz. **30**: 217–251. *pl. 14*. 1900.

in the study of spore formation in *Pilobolus* and *Fuligo* that a differentiation of the cytoplasm might occur during the process of cleavage. He found "hyaline areas" occurring midway between each pair of nuclei. According to his account the cytoplasm appears as if the protoplasmic mass had contracted about each nucleus as a center, thus leaving irregular, furrow-shaped, less dense spaces in the middle region between the two nuclei.

In *Cobaea* the less dense areas referred to above are practically free from any granular masses, and appear very clear. The term "hyaline areas" has not been used because the discussion and figures by Harper concerning the somewhat similar regions in the dividing cells of the fungi indicate a condition of greater transparency than is evident in *Cobaea*. These areas also do not appear so markedly wedge-shaped as those shown by Harper in *Fuligo* (*f. 8*). They are, however, in general form, not at all unlike that shown by the same author in his *f. 9*. Aside from these differences, the description of the "hyaline areas" in *Fuligo* and *Pilobolus* might be applied directly to the less dense areas in *Cobaea* without any alteration.

The appearance of such cytoplasmic differentiation in these widely separated forms would seem to be of significance in establishing the similarity of the processes concerned in the divisions by furrowing, and would also give strength to the idea that they are worthy of all of the recognition given them by Harper in the fungi. Since these less dense areas may be found to occur in both dicotyledons and fungi, it must be remembered that the conditions under which they are found are quite similar. In all cases they appear in connection with the cytoplasmic division of a multinucleate cell in which cell-plates are not formed. In all instances so far reported they bound off a single nucleus and never a group of nuclei. They are also the early indicators that the process of cleavage will result in uninucleate masses with approximately equal amounts of cytoplasm.

A comparison of the pollen-mother-cells of the two forms with reference to the breadth of the progressing furrow will show that they are much more narrow in *Cobaea* than in *Nicotiana*. A further comparison of the maximum thickening of the cell-walls in the two forms shows that it reaches a thickness of one-tenth of

the pollen-mother-cell in *Nicotiana*, while in *Cobaea* it thickens to only one fifteenth of the mother-cell diameter.

If the cell-wall material is colloidal in nature, the degree of its plasticity would be related to the amount of swelling due to imbibition. This suggests a possible relation between the amount of thickening in the wall and the breadth of the furrow. If in a pollen-mother-cell such as that of *Nicotiana* there is an almost negligible degree of resistance of the cell-wall to the forms assumed by the protoplast, as suggested by C. H. Farr, the pollen-mother-cell-wall of *Cobaea*, which thickens less, might be conceived of as producing a greater resistance to the cell within. The relative surface tension of the protoplast, together with the less plastic cell-wall, might prevent the early rounding up of the lobes of the mother-cell of *Cobaea*, and thus decrease the breadth of the furrow.

The conditions reported in the microspore formation of *Drosera*, by Levine,* suggest a further application of this idea. In that case no cell-plates could be determined during the division of the cells, and they did not present the marked characteristics of a process of division by furrowing. Levine states: "if furrows are present in *Drosera* they must be extremely narrow like those shown in the slime moulds by Harper ('00, '14), which proceed from the periphery to the center of the cytoplasm." The cell-wall of the pollen-mother-cell of *Drosera* thickens to only one-twenty-second of the diameter of the protoplast, and if the previous suggestions are assumed, would exert an even greater degree of resistance to the protoplast than that of *Cobaea*. This may perhaps be great enough to account for an extremely narrow furrow. The fact that the pollen-mother-cells do not separate after cell-division is completed, but form a tetrahedral pollen-grain, may also be of significance in this relation.

It has been observed that some forms of amoeba before making contact with a food particle send forth strands of protoplasm, or pseudopodia, and surround the food. A fusion of these pseudopodia at their free ends or edges results in the complete enclosure of the food. In *Cobaea*, as has been previously stated, the advancing tips of the furrows are seen first between the spindle-

* Levine, M. Somatic and reduction divisions in certain species of *Drosera*. N. Y. Bot. Gar. Mem. 6: 127–147. *pl. 16–19.* 1916.

fibers, and later they appear to surround them. These observations, together with the appearance of the spindle-fibers throughout cell-division and after division is completed, lead to the conclusion that the fibers are first surrounded and then severed. In considering such a progressing furrow with relation to the fibers, the behavior of the amoebae toward their food particles suggests itself as an analogy. The apparently very elastic plasma-membrane plays a prominent part in both instances. In the process of furrowing the spindle-fiber corresponds to the food particle. It does not seem entirely inconceivable that the advancing edge of the furrow, amoeba-like, may approach a fiber to within a certain distance and then send forth projections which first surround it and finally cause it to separate at its middle point.

The cleavage in *Cobaea*, as has been shown, is directed with reference to the distribution of the nuclei. It seems quite possible, as was suggested by Harper for *Fuligo* and *Pilobolus*, that the nuclei may control the orientation of the furrows, and that the formation of the less dense zones in the cytoplasm is a visible expression of the activity of the nuclei. If to these assumptions are added the suggestions of C. H. Farr, concerning the diffusion of soluble ions from the nuclei along the paths of the fibers, a possible explanation for an amoeboid activity suggests itself. If the fibers mark the paths of diffusion, the compounds formed by the meeting ions would be most concentrated around the fibers in the exact equatorial planes. It does not then seem unthinkable that in these regions of highest concentration the substances may be in the necessary condition to contribute to the development of the plasma-membrane, and that in this manner they determine the position and direction of the penetrating furrows.

To Dr. R. A. Harper I wish to express my appreciation for advice and inspiration during the progress of this study.

DEPARTMENT OF BOTANY,
COLUMBIA UNIVERSITY

Explanation of plate 14

The figures were drawn with a Spencer 1.8 objective and ocular 4, with a tube length of 170 mm. The magnification is about 1,971 diameters.

FIG. 1. Mother-cell after second nuclear division. Nuclei are organized, spindles inflated, and wall thickened.

FIG. 2. An early stage in the furrowing process, showing thickened fibers and the first appearance of less dense areas.

FIG. 3. Furrows penetrating deeper, fibers undisturbed in position, and tips of furrows between fibers.

FIG. 4. A section with deeper furrows, showing no penetrating tips in the less dense areas.

FIG. 5. Another section from the cell represented in FIG. 4, between that section and the fourth nucleus, showing penetrating tips of furrows between the fibers.

FIG. 6. Narrow continuous furrows, tips of furrows, and the beginning of a central triangular area.

FIG. 7. Late stage in division, showing continuous fibers, surrounded fibers, central triangular area, and the rounding up of the daughter-cells.

Apogamy in Osmunda cinnamomea and O. Claytoniana

ELIZABETH DOROTHY WUIST BROWN

(WITH 10 TEXT FIGURES)

The occurrence of apogamy in *Osmunda cinnamomea* L. and *O. Claytoniana* L. is of especial interest, since the only reported case of apogamy in this genus is given by Leitgeb.† He does not state definitely in which species he observed apogamy but presumably it was in *O. regalis* L. His observations have never been confirmed, although attempts have been made by workers to induce apogamy in this fern under varied cultural conditions.

The cases of apogamy described in this paper occurred in cultures of *Osmunda cinnamomea* and *O. Claytoniana* with which, together with *O. regalis*, experiments were made during the years 1916–18 in the Osborn Botanical Laboratory of Yale University. The writer is especially indebted to Professor A. W. Evans for many helpful suggestions and criticisms.

MATERIAL

The spores of *O. regalis*, *O. cinnamomea* and *O. Claytoniana* were collected from two sources: from sporophytes growing on lawns about New Haven, Connecticut, and from sporophytes growing under natural environmental conditions in Beaver Swamp, a short distance from that city. No differences were observed in the growth and development of the prothallia from the two sources.

Collections of fertile fronds were made in late June and cultures were made early in July. The cultures were made by sowing the spores on 26 c.c. of Prantl's and Knop's nutrient solutions and their modifications, to which had been added a drop of a 1 per cent solution of ferric chloride, in small glass capsules.

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* Contribution from the Osborn Botanical Laboratory.

† Die Sprossbildung an apogamen Farnprothallien. Ber. Deutsch. Bot. Ges. 3: 169–176. 1885.

The formulas for these solutions are as follows:

I. PRANTL'S SOLUTION (PRANTL '81)		II. KNOP'S SOLUTION	
K_2SO_4	0.70g.	$MgSO_4$	0.25g.
NaCl	0.23g.	$Ca(No_3)_2$	1.00g.
$CaSO_4$	0.70g.	K_2HPO_4	0.25g.
$MgSO_4$	0.50g.	KCE	0.12g.
Na_2PO_4	0.50g.		
NH_4NO_3 solution, 0.064 per cent	20 c.c.		

In the following modified solutions the items not mentioned are the same as in the corresponding unmodified solution:

I. PRANTL'S SOLUTION
I *a*. NH_4NO_3 omitted
I *b*. K_2SO_4 omitted
I *c*. NaCl omitted
I *d*. $CaSO_4$ omitted
I *e*. $MgSO_4$ omitted
I *g*. NaCl and Na_2PO_4 omitted

II. KNOP'S SOLUTION
II *a*. $Ca(NO_3)_2$ omitted

After the spores had been sown the cultures were placed before an east window and the culture solutions were not renewed. It was only during the period of germination that the cultures were exposed to the direct rays of the sun for a short time each day. If left longer the solution became heated and the prothallia died.

DEVELOPMENT OF PROTHALLIA AND SEX ORGANS

Germination, in all three species, began in a few days after the spores were sown.

O. regalis.—Three weeks later the prothallia of this species varied in the different cultures from four to fifty-nine cells, the greatest irregularity in size occurring in cultures of I*c*. On the whole greater growth occurred in cultures of the modified than in those of the unmodified solutions, and this was especially true in the case of I*a*. Here the amount of nitrate present was evidently sufficient to meet the needs for the growth of the prothallia and the effect of the unbalanced solution tended at first to stimulate rather than retard the growth. However, the reverse was true in the later development of the prothallia, for at the end of the fourth month in I*b*, I*c*, I*d*, I*g*, and II*a* the majority of the prothallia were dead; in I*a*, I*f*, and I*g*, although the prothallia were alive, growth was much slower.

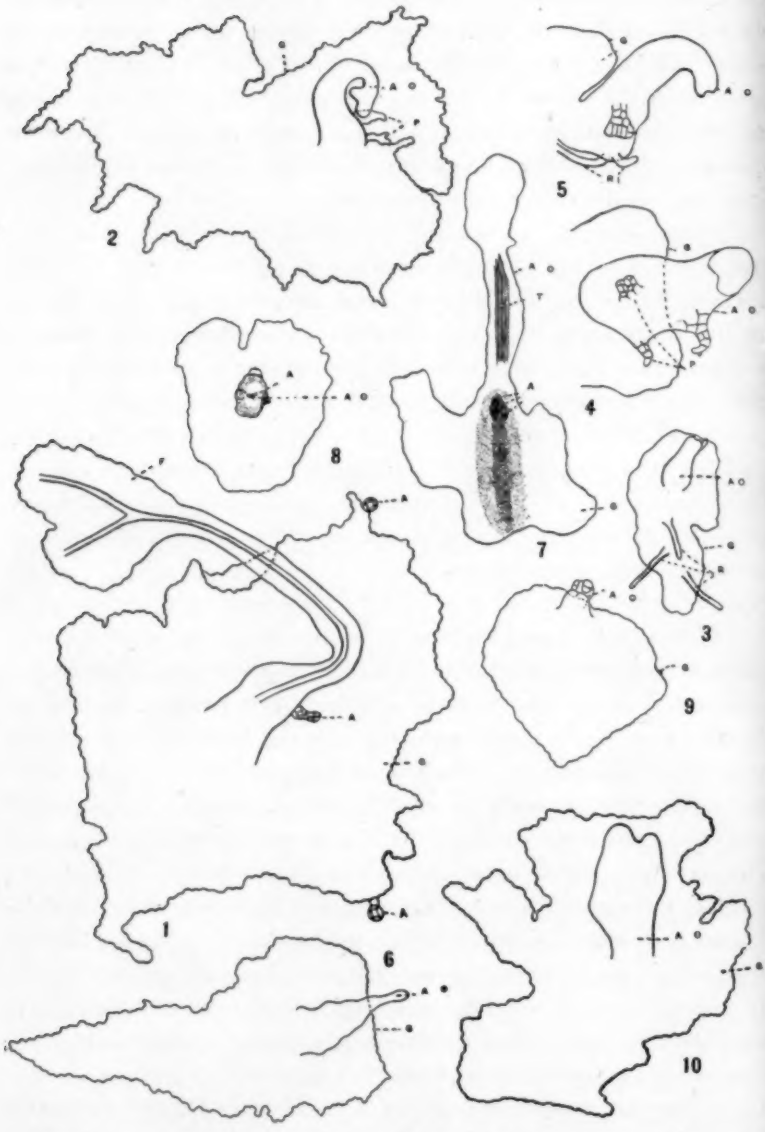
Campbell* states, "in . . . *O. regalis* it is quite common to

* Mosses and Ferns, p. 340. London. 1895.

have the first transverse wall followed by a longitudinal wall in each cell, so that the four primary cells are arranged quadrantwise." While in general this was the order of development, yet in some of the cultures a filamentous stage of two and three cells was formed before longitudinal division took place. Even in those cases where the four primary cells were arranged quadrantwise the prothallia tended to assume an elongated form and not a cell mass at first. In I*d* the prothallia were very broad and frequent branching occurred at the expanded apices of the prothallia. In I*e* and I*f* the growth was very irregular, some of the prothallia tending to assume an elongated form and others a broad form. Branching in these cultures was rare; in I and II*a*, however, it was common, the branches often occurring as filamentous outgrowths at the bases of the young prothallia, which were decidedly filamentous in form. In some cases this was so marked that a reversion of the prothallia at its apex to a filamentous condition took place. Large heart-shaped prothallia, monoecious in most cases, were present in the unmodified solutions. No cases of apogamy in the species were observed.

O. cinnamomea.—Growth in this species during the first three weeks was not so rapid as in *O. regalis*, for the largest prothallia were only thirty-four cells in size and the smallest two cells. As in *O. regalis* greatest growth took place in I*a*, while least growth occurred in I*b* and I*f*. The early divisions of the prothallia were in keeping with the previously quoted statement of Campbell. However, in many cases in I*a* the filamentous stage consisted of from three to five cells. The young prothallia in most of the cultures were broad in form, sometimes a mere cell mass. In the case of the prothallia in II (Knop's unmodified solution), while the initial divisions were the same, there was more of a tendency for the young prothallia to become elongated and in rare cases a filamentous stage, as many as seven cells in length, was formed before longitudinal divisions took place.

A greater irregularity in the form of the young prothallia occurred in the cultures of the various modified solutions than in the same cultures of *O. regalis*. In I*a*, I*c*, I*d*, I*f* and I*g* the form of the young prothallia was very irregular, this being especially pronounced in I*a* and I*c*. Greater regularity of form occurred



FIGS. 1–7. Apogamous outgrowths of *Osmunda cinnamomea*. FIGS. 8–10. Apogamous outgrowths of *Osmunda Claytoniana*. *AO*, apogamous outgrowths; *a*, archegonia; *a'*, antheridia; *f*, leaf; *g*, gametophyte; *r*, rhizoid, *t*, tracheids.

in I*b* and I*e*. In II*a* the regularity of form was very striking. However, at the end of eight months the greatest irregularity of form was shown by the prothallia of I*a* and I*c*. Many of these were elongated plates of cells with the margins of the apices extremely irregular. Branching of the prothallia occurred in the cultures of the following solutions: I*a*, I*b*, I*c*, I*d*, I*e* and I*g*, being especially marked in I*a*, I*b*, I*c* and I*d*.

Sexual organs, both male and female, developed in various cultures. That some of these were normal was shown by the presence of young sporophytes, which developed only in the unmodified solutions after the nutrient solution had been renewed.

Apogamous outgrowths, developed on prothallia in cultures of the following solutions, eight months and one week (March 9, 1917) after the spores were sown (FIGS. 1–6): I, I*a*, I*b* and I*e*. In another attempt to induce apogamy, prothallia were transferred from cultures of I (Prantl's unmodified solution) to I*a* four weeks after the spores were sown. One case of apogamy in these cultures was observed (FIG. 7).

O. Claytoniana.—At the end of three weeks the average size of the prothallia of this species in the different cultures varied from one to thirty-three cells. As in *O. regalis* and *O. cinnamomea* the greatest growth occurred in I*a*; least growth occurred in I*c*. No filamentous stage was present in many of the prothallia of the unmodified solutions, a longitudinal wall having been formed in the first cell. In other prothallia the filamentous stage varied from five cells in I*c* and I*f* to six cells in II*a*, seven cells in I*c* and II*a* and eight cells in I*c*.

The young prothallia in the cultures of the unmodified solutions I and II and the modified solutions I*a*, I*b*, I*c*, I*g* and II*a* were regular in form, being somewhat elongated. But in I*d*, I*e*, I*f* and II*a* the form of the majority of the prothallia was very irregular; in some cases they were broad, in others elongated. The older prothallia (March 19, 1917) in the cultures of I*a*, I*b*, I*d*, I*g* and II*a* showed the greatest irregularity of size and form. Those of I*d* and I*g* were the smallest in size, while those of I*a* and I*b* were the most irregular in form, some of the prothallia of I*a* being irregular plates of cells.

No branching of the prothallia was observed in the cultures

of I*b* and II while in I, I*a*, I*c*, I*d*, I*e* and I*f* it was rare. In the cultures of I*g* branching of the prothallia was very common. In all cases observed the branching of the prothallia occurred in the younger stages of the development.

Sexual organs were found in the unmodified solutions, while in the modified solutions they were formed only on the prothallia in I*a* and I*b*. However, in the latter only a few sexual organs were observed. Normal sporophytes developed in some cultures of the unmodified solutions after the nutrient solutions had been renewed, and three apogamous outgrowths occurred on prothallia in I*b* (FIGS. 8–10).

DESCRIPTIONS OF THE APOGAMOUS OUTGROWTHS

The apogamous outgrowths in *O. cinnamomea*, as previously stated, developed on prothallia in cultures of I, I*a*, I*b* and I*e*. One developed also on a prothallium which had been transferred from I (Prantl's solution), four weeks after the spores were sown, to I*a*.

The prothallium in a culture of I (FIG. 1), upon which the apogamous outgrowth occurred, was irregular in shape and no sinus was present. Two antheridia developed from marginal cells, one in the expanded apex and one near the base of the prothallium. One of the antheridia was stalked and the other sessile. The prothallium was one cell thick, except for a small region in the center where the meristem is usually formed. In this region a swelling occurred which continued to grow, forming a cylindrical process several cells in thickness. Gradually it assumed the shape of a young leaf and finally developed into a normally appearing leaf consisting of a petiole and a blade bearing a forking rib. On one side of the petiole near its enlarged base an archegonium which appeared normal developed.

The apogamous outgrowth which occurred in a culture of I*a* developed in the same manner as the one just described. This prothallium, also, was approximately the same size and shape (FIG. 2); however, no antheridia or archegonia were formed.

The apogamous outgrowth found in a culture of I*b* developed on a prothallium which was small, elongated and regular in shape. No sinus was present and from the meristematic region near the apex of the prothallium the apogamous outgrowth was formed. It began as a swelling which developed into a cellular mass.

Swollen at its base it narrowed and then enlarged into an apex which was slightly lobed (FIG. 3). This structre continued to elongate and formed a flat, cellular mass which was lobed (FIGS. 4, 5). From near its base and on one side of the structure proliferations of a thallus-like character developed.

The prothallium in the culture of I*e*, which gave rise to the apogamous outgrowth, was wedge-shaped with an obtuse apex without a sinus (FIG. 6). As in the previous cases described the apogamous outgrowth developed as a swelling from the meristematic region. This swelling continued to grow, forming a cylindrical process several cells in thickness which became somewhat narrower as it developed.

An apogamous outgrowth formed on a prothallium which had been transferred from I to I*a*, four weeks after the spores were sown. This prothallium (FIG. 7) was broad and irregular, one lobe being much larger than the other. A meristem was present from which archegonia, normal in appearance, developed. From the margin of the prothallium, where the sinus is usually formed, the prothallium continued to grow into a cylindrical cellular structure, which finally broadened into a flat thallus-like body one cell in thickness with a rounded apex. Tracheids were formed in the narrow thickened portion.

All three cases of apogamy in *O. Claytoniana* were observed in cultures of I*b*, where they developed as cellular masses on the prothallia (FIGS. 8–10). One of these cellular masses, formed as a swelling from the meristem near the center of a heart-shaped prothallium which was distinctly notched, bore on the side near its apex an archegonium (FIG. 8). Another of these cellular masses (FIG. 9) was formed a little to one side of the center of the meristem and near the expanded apex of a prothallium. This outgrowth began as a swelling of the tissue, which was triangular without a sinus, and developed into a mass whose apex was slightly lobed. From one side a proliferation of a thallus-like character developed. The third cellular mass was formed on a very irregular prothallium (FIG. 10). Although the margin was greatly indented in places no apica sinus was present. The apogamous outgrowth, as in the other two cases, appeared first as a swelling of the meristem and then developed into an irregular, cylindrical cellular mass whose apex was distinctly bilobed.

Regeneration in Sphaerocarpos Donnellii

H. W. Rickett

(WITH TWENTY-FIVE TEXT FIGURES)

Regeneration, or the production of adventitious shoots from the vegetative tissue, has been described in *Sphaerocarpos* by Leitgeb (4), C. and R. Douin (2), and Goebel (3). Leitgeb describes regeneration in *S. Michelii* Bell. (*S. terrestris* Sm.) as occurring from both the lobes and the midrib of the thallus. It results from the growth of a single cell into a cylindrical body, whose tip gradually broadens out and becomes flat, forming the normal plant body. As in the case of sporelings, sex organs are formed very early—in some cases before the young shoot has assumed the flat shape.

The Douins (2), studying *S. Michelii* and *S. texanus* Aust. (*S. californicus* Aust.), observed regeneration taking place from the midrib and from the involucres, and state that it probably occurs also from the lobes, though this was not seen by them. Regeneration is most marked in connection with the female thalli. When these are destroyed by drought, the midrib remains alive for some time, and if a period of humidity follows, each fork of the midrib elongates, forming more or less numerous lobes and involucres. Regeneration also occurs from the involucres, when these are accidentally bent over and brought into contact with the soil. Certain cells of the involucre in these cases multiply and give rise to new thalli. The Douins' figures show such plants arising from around the opening of the involucre, in exactly the same way as is illustrated in my Fig. 18. The regenerated thalli are somewhat different from the old ones, especially in the case of the male, showing dorsal lobes, whose form leads the authors to conclude that they are modified involucres.

Goebel (3), working with *S. Michelii* (possibly mixed with *S. texanus*, if the latter species is found throughout Europe as it is in France), found that regeneration occurs when portions of the

thallus, especially the involucres, are broken off or partly broken off, and are in contact with the soil. Regeneration is most easily observed if separated portions of the involucres are cultivated in water. Shoots may be produced either on the inside or on the outside of the involucre, and rhizoids are produced at the same time, especially in the neighborhood of the shoots. When shoots develop on the inside of the involucre, it is necessary for them to curve about so as to emerge; if formed on the outside of the involucre, they grow straight outward. A shoot is formed as a cell mass arising from a single cell. At the tip of this body is formed the growing point. Right and left from this, flat wings develop. Sometimes a long germ-tube is first formed, consisting of many cells. In such a case, the whole structure resembles a sporeling, except that the formation of the flat plate at the end of the germ-tube is not at right angles to the germ-tube, but simply a spreading out and flattening of the latter. The history, except in a few cases, is not so simple as that described by Leitgeb, the wings not necessarily lying in one plane, and the formation of the flat plate resulting from the spreading out of the first cylindrical body. Sometimes one of the wings goes on to develop into a thallus, apparently because the development of the growing region between the two wings was arrested. Goebel compares the formation of these adventitious shoots with spore germination, and emphasizes the fact that they may develop either almost exactly as does a sporeling, namely by the formation of a flat plate of cells from the terminal group of cells of the germ-tube, or by a direct and simple flattening out of the primary cell mass, which fact shows of how little value is any sharp distinction between these two methods in a discussion of spore germination.

I first noticed the occurrence of regeneration in searching for germinating spores in soil cultures of *S. Donnellii* Aust. Many small plants which I picked up proved to have no spore wall attached at the basal end, and in some cases were found instead to be attached to old dead portions of tissue. In these cases the plants were of a ribbon-like form, broadening out a little at the anterior end. In cultures made later for the purpose of obtaining regeneration, the young plants were broader and less ribbon-shaped. The light conditions under which these latter plants

had developed were more favorable. In the cases first noted the young plants were growing among older plants, which overshadowed them to a large extent, and the elongated ribbon form is probably a resultant of these conditions.

Regeneration also occurred from the involucres of several female plants which were being cultivated singly on soil. Conditions here were such as to produce the extreme leafy form of the thallus described in a previous paper (5); as the posterior part of the thallus died, small masses of cells protruded from the involucres in this region and later grew out into young thalli.

Attempts were made to induce regeneration by artificial means, such as the wounding of the female thalli. In cases in which involucres or lobes were almost or completely separated from the plant body, regeneration occurred abundantly, though not usually at points showing any definite relation to the cut surfaces. The rest of the plant continued to grow in a normal manner, although occasionally adventitious shoots were formed on the midrib, often near places where portions had been cut off. I have never observed regenerated shoots to arise directly from one of the wounded surfaces. Very frequently rhizoids developed from the cut end of the separated portion of the thallus; these appeared without any spatial relation to the adventitious shoots and sometimes before the latter became evident.

Attempts were also made, in every case unsuccessfully, to induce regeneration, using the same or similar methods, from the sex organs, and also from young sporophytes.

The occurrence of regeneration is frequent in cultures, especially from the female thalli, and seems to be a regular method of vegetative multiplication, rather than merely a response to abnormal conditions. After the development of sporophytes, the mother plants often die in large part, and growth continues after a time by means of regeneration from their surviving portions. C. Douin (1), describing the life history of *S. Michelii* under natural conditions in Europe, states that the old thalli are usually buried by the tilling, and that the spores produced on these plants germinate with the spring rains. If regeneration occurs as abundantly under natural conditions as it does in cultures, it seems not impossible that the old thalli thus buried in the spring

may continue their growth by the production of adventitious shoots.

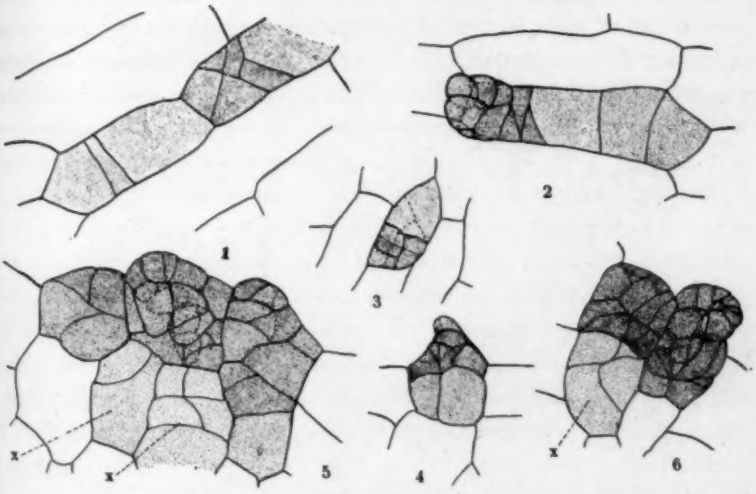
My observations seem to warrant the conclusion that regeneration is a rather common phenomenon in *Sphaerocarpos*, resulting from particular nutritive conditions in the thalli or in parts of the thalli, rather than merely from a direct response to occasional accidental stimuli.

The descriptions that follow are based on data obtained from female plants, these being more abundant and more convenient for study than the male. In a few male plants that were studied, the phenomena observed were similar to those here described. The plants produced by regeneration were in all cases of the same sex as the parent plant. Several cultures of female plants, which were started by sowing involucres separated from the thalli, on soil, are still growing vigorously at the present time, nearly twelve months afterwards, and are still purely female.

In order to study in detail the method of formation of the adventitious shoots, involucres, lobes, and small portions of the midrib were cut off and placed on moist filter paper in petri dishes. At the end of two weeks or thereabouts (in one case after six days), these small pieces of tissue were covered with outgrowths in various stages of development. They were then removed, killed by placing in a dilute solution of chrom-acetic acid (chromic acid, 0.3 g.; glacial acetic acid, 0.7 cc.; distilled water, 99 cc.), stained in eosin, and mounted in glycerin.

When regeneration is about to occur, the contents of a single cell become more dense and richer in chlorophyll content. Such a cell may be isolated, or there may be a group of similar cells adjoining or in close proximity to one another. Cell division then occurs, without an accompanying growth of the mother cell. The relative position of the walls formed in these divisions is quite variable. FIGS. 1, 2, 3, 4, 13, and 14 represent groups of cells formed in this way. It makes no particular difference whether the original cell was on the edge or in the middle of the tissue of the parent plant, nor does its size or shape have any influence on the course of development. Very commonly, indeed in the majority of cases, the walls are set in at acute angles to each other, and in the case of the involucral cells these divisions

occur mostly at one end of the mother cell, the other end being divided into only two or three comparatively large and clear cells (FIGS. 1, 2). The end cell of a row of cells formed in this way suggests a wedge-shaped apical cell, cutting off segments alternately to right and to left. The process is, however, too variable to justify the conclusion that the growth of adventitious shoots is regularly due at first to the activity of such an apical cell.

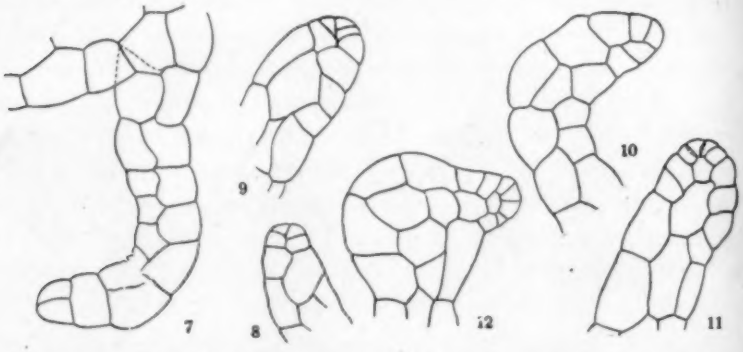


FIGS. 1–6. Single involucral cells dividing to form adventitious shoots. The shading indicates the extent of the original mother cells, the darker portions representing those of the densest contents. FIG. 1. Two adjacent mother cells at an early stage of regeneration. FIGS. 2, 3. The young shoots beginning to project above the surface of the parent tissue. FIG. 4. Shoot arising from a marginal mother cell. FIGS. 5, 6. Shoots arising from adjoining marginal mother cells: *x*, *x*, adjacent involucral cells also dividing. FIGS. 1–4, 6, × 150; FIG. 5, × 200.

As cell division continues, the cell mass so formed begins to protrude above the surface of the parent tissue at one end of the mother cell (FIG. 2). This seems to be due simply to a bulging up of the mass of cells, followed by cell divisions in planes more or less nearly parallel to the surface of the tissue from which the shoot is growing. If regeneration occurs from the margin of the parent tissue instead of in the middle, this bulging out commonly does not occur; the young plant grows straight out from the margin, and gradually curves so as to bring its distal portion into a more erect position.

After the young plant has thus become a distinct outgrowth from the parent tissue, cell divisions occur in many planes, so that there is formed a compact mass of cells several cells thick in each dimension. The form of this mass is globular or cylindrical, and there is no longer any evidence of the existence of an apical cell (FIGS. 5, 6).

The only exceptions found to this history were in the first cases of regeneration noted, mentioned above, in which each young plant grew out as a long ribbon. Presumably this took place by the continuation, after the cell mass had once bulged out from the original containing wall, of divisions similar to those which had cut up the original mother cell. The cell at the tip of



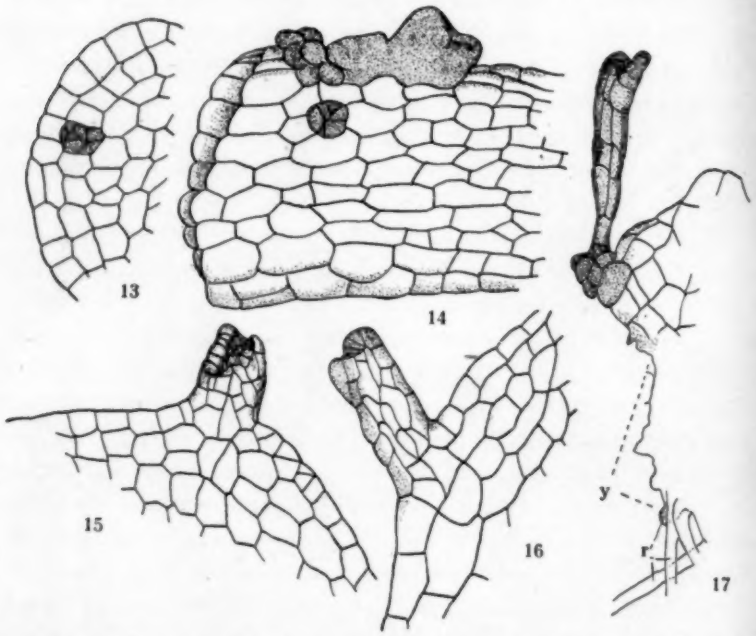
FIGS. 7–12. The tips of filamentous adventitious shoots. FIGS. 8–10. Development by means of a two-sided apical cell. FIGS. 11, 12. Broadening of the apical region into the thallus-plate. All, × 150.

such a ribbon-shaped growth had in most cases exactly the appearance of a two-sided apical cell, cutting off segments alternately to right and to left. The segments themselves redivided only occasionally, so that a narrow shoot, two cells wide and one cell thick, resulted. The tips of such shoots are illustrated in FIGS. 7, 8, 9, 10. These young plants finally broadened out at the tip (possibly in response to more favorable light conditions), and the ordinary flat plate-shaped thallus resulted. As soon as the broadening had occurred, an apical cell could no longer be distinguished, further growth being due to a group of small meristematic cells on the margin of the plate, either in an apical or in a lateral position (FIGS. 11, 12, 19).

This history bears a striking resemblance to that of the sporelings described in a previous paper (**5**), which developed from spores sown in a nutrient solution. These sporelings were marked by the production of an excessively long germ-tube, which, when conditions were favorable, gradually broadened out into the thallus-plate. In the cases of some sporelings (**5**, *f. 35*), ribbons were formed which were almost identical in appearance with those just described as arising by regeneration. Obviously the unusual form in each case bears much the same relation to the normal or common method of development. All gradations are found between the two methods among both sporelings and adventitious shoots, the latter, however, being, so far as my observations have shown, by far the more variable.

In cases in which several adjoining cells start regeneration, it seems that the growths produced by each may become fused together into one new plant. This is rather difficult to determine, but it is certain that one often sees many contiguous cells starting to divide, while there are rarely as many plants formed on a single portion of tissue as would represent the development of all these cells into separate plants. The possibilities suggested are that fusion may occur, two or more cell masses growing together into one structure, or that the development of some of these cell masses may be checked. FIG. 14 shows adventitious growths resulting from the division of groups of adjacent cells. In FIGS. 15, 16, and 19, the young plants seem to have developed each from a single marginal cell of a lobe, the base of the shoot not being much wider than a single marginal cell. FIG. 18 represents several plants arising by regeneration from the margin of the opening of an involucre. Here also each plant seems to have developed from a single cell. FIGS. 5 and 6 show similar groups of marginal cells at an earlier stage in regeneration. The cell masses resulting from the division of individual marginal cells can be fairly readily distinguished, and seem to be each in process of forming independent shoots; but there are other cells (*x*) adjoining these which have also divided, and it is impossible to say whether the cell groups thus formed will also give rise each to a separate plant or whether they will merely contribute to the cell masses formed from the marginal cells.

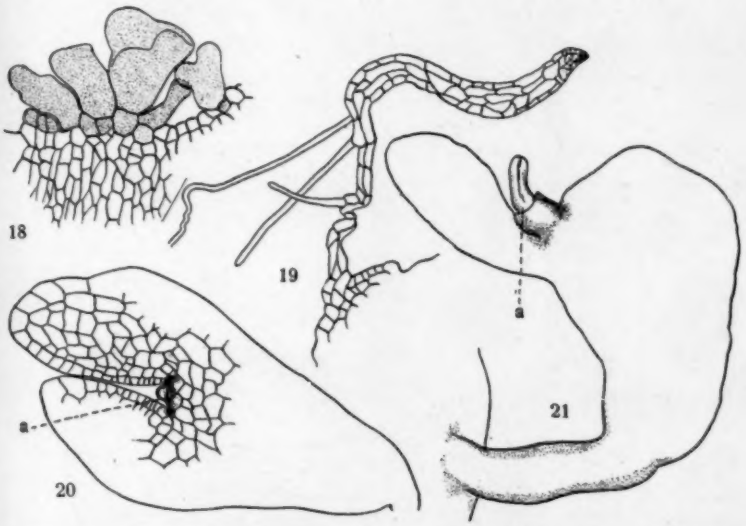
Very often, the surrounding cells being largely dead or dying, the cells which form the new plants assume a globular form and stand out from the surrounding tissue. This is especially true when regeneration occurs from the midrib. Such a case is shown in FIG. 17. Here also there is a strong suggestion that a group of cells is concerned in the production of a single new plant.



FIGS. 13–17. The further development of shoots produced by regeneration from involucres and lobes. The shading indicates the density of the cell contents in the new plants. FIG. 13. Regeneration from a single cell of a lobe. FIG. 14. Cell masses produced by the division of a number of adjoining mother cells of an involucre. The cell contents were so dense that the cell walls could not be distinguished. FIGS. 15, 16. Regeneration from the margins of lobes. FIG. 17. Regeneration from the midrib: *y*, cut surface; *r*, rhizoids. All drawn from living material, × 75.

In the course of the usual history, after the young plant has developed into a small globular or cylindrical mass, a flat plate is formed as the result of the continued division of a group of cells at the tip of the structure. FIGS. 15 and 16 represent cases in which this process is taking place at an early stage; in FIGS. 17, 21, 22, and 23 the original cell mass has developed into a long and

comparatively slender body, in one case (FIG. 17) strongly suggestive of the germ-tube formed as a result of spore germination. As in the latter process, the thallus-plate is at first usually cup-shaped or trough-shaped (FIG. 15), and the growing point may lie in a median or in a lateral position. The tissues formed to right and left of the apical point grow rapidly, so that the latter lies at the base of a deep apical notch (FIGS. 20, 21, 22). As in the case of the sporeling, the first sex organ appears very early



FIGS. 18–21. Young plants produced by regeneration. FIG. 18. Shoots arising from a number of adjoining marginal cells of the involucre. The cellular structure of the shoots is not shown. FIG. 19. Filamentous shoot produced from the margin of a lobe. FIG. 20. The terminal plate of a young plant, showing the apical notch: *a*, young archegonium. Fig. 21. Young shoot, consisting of a cylindrical basal portion and a terminal flat plate: *a*, archegonium enclosed in young involucre. FIGS. 19–21 drawn from living material. Figs. 18, 19, × 35; FIGS. 20, 21, × 75.

(FIG. 21), being formed immediately behind the growing point. Presumably an apical cell, or group of initials, is developed in the growing region just previous to the formation of the first sex organ, since from this point the history of the adventitious shoot is identical with that of a typical thallus (5).

In the case of some of the male plants studied, the young plant arising by regeneration produced only a few antheridia,

and assumed a very elongated form, with few lobes. Such a plant is shown in FIG. 23. Similar results were obtained from female plants by allowing regeneration to occur under water (FIGS. 24, 25). In one case (FIG. 24), no sex organs were produced, and scarcely any lobes. In another case (FIG. 25), the tip of the plant reached the surface of the water and there began to take on

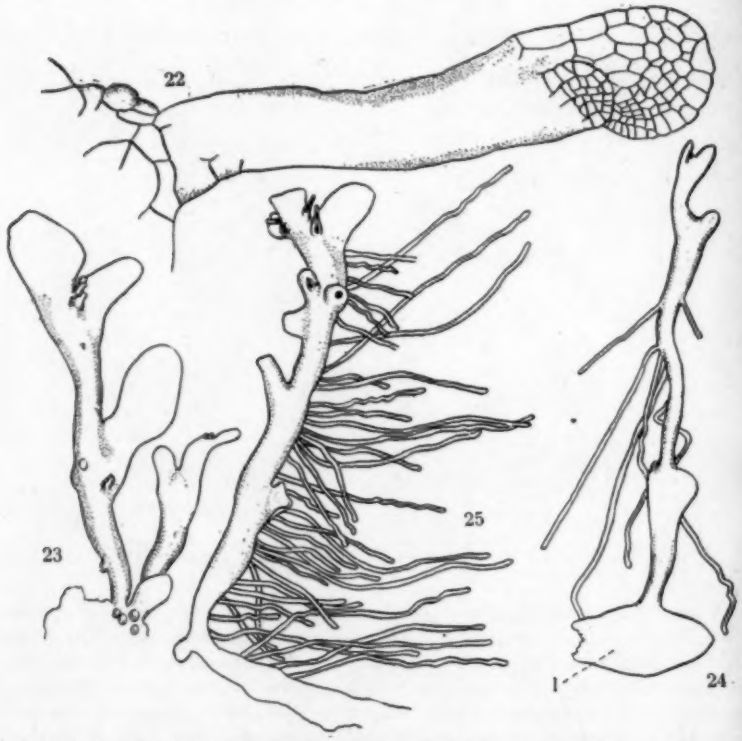


FIG. 22. The apical notch formed laterally on a long cylindrical cell mass. FIG. 23. Young plant, with antheridia, produced by regeneration from the lobe of a male plant. FIGS. 24, 25. Shoots developed from portions of female plants cultivated under water: *l*, parent lobe. All drawn from living material. FIG. 22, × 100; FIGS. 23–25, × 20.

more nearly the ordinary appearance. Production of rhizoids was especially abundant in this latter case.

SUMMARY

1. Regeneration in *Sphaerocarpos Donnellii* may occur from any vegetative tissue of the thallus, either when the thallus as a

whole is partly dead, or when portions of it are separated or partly separated from the rest under conditions favorable for growth.

2. Plants produced by regeneration originate for the most part in a single cell, which divides irregularly to form a cell mass whose shape is dependent on environmental conditions. It is possible that in some cases this cell mass may originate from several adjoining cells of the parent plant instead of from one cell only.

3. There is a tendency towards the formation of a two-sided apical cell in the early stages, this being most marked when conditions are comparatively unfavorable. This tendency may lead to the formation under unfavorable conditions of a long, narrow, ribbon-shaped plant.

4. The development of the first cell mass, globular, cylindrical, or ribbon-like, into a typical thallus takes place in a manner entirely analogous to the development of a mature thallus from the germ-tube produced by a spore on germination.

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A misconception as to the structure of the ear of maize

PAUL WEATHERWAX

(WITH SIX TEXT FIGURES)

It is a fact of common knowledge and general interest that the rows of an ear of corn regularly occur in even numbers. By the layman this has usually been regarded as one of Nature's curiosities, not necessarily to be explained in any way; but the botanist long ago found it to be the expression of a morphological characteristic of the whole tribe (Maydeae) to which maize belongs.

Ordinarily the spikelets in all parts of both inflorescences of the maize plant are borne in pairs, one sessile and the other pedicelled. The fundamental structural unit of the ear of corn is a row of these paired spikelets, or, in other words, a pair of rows of grains, each spikelet producing one grain. As a rule there is no ascertainable difference between the two grains produced in a pair of spikelets, but there is abundant evidence that the sessile spikelets are responsible for one row and the pedicelled ones for the other.

It often happens that an ear has more rows at the base than at the tip, the difference in number being always two or a multiple of two. When the difference in number is two, both rows are dropped at exactly the same distance from the base of the ear; if the difference is more than two, two rows may be dropped at one distance from the end of the ear, two at another, and so on. Thus, no part of the ear is ever left with an odd number of rows.

The natural inference has been that these irregularities are due to the discontinuance of one or more rows of paired spikelets, an explanation apparently in harmony with most facts and theories centered in this unique structure. It is somewhat surprising, therefore, to find in connection with a recent theory* as to the origin of the ear of maize, a new explanation of this irregularity in the rows.

* Collins, G. N. Structure of the maize ear as indicated in *Zea-Euchlaena* hybrids. Jour. Agr. Research 17: 127–135. *pl. 16–18 + f. 1.* 1919.

FIG. 1. An ear with eighteen rows at the base and ten at the tip.

A cardinal point in Collins's new theory of the origin of the ear is that each pair of spikelets is yoked structurally with another pair on the opposite side of the ear; and the statement is made (pp. 133–134) that a reduction in the number of rows between the base and the tip of the ear is due not to the discontinuance of a row of pairs of spikelets, but to the loss of the pedicelled spikelets from yoked pairs for a part of the length of the ear. No criticism of the general bearing of the theory is intended here, but the corollary statement as to the manner of the loss of rows cannot go unchallenged.

Just what technique was employed in securing this anomalous bit of evidence is not explained, except that many ears are said to have been examined, and reference is made to tassels having pistillate portions. In external appearance, an ear of corn is a very deceptive thing, and peculiar technique is sometimes necessary to bring out its true structure. The semblance of rows on the surface, being largely due to the adjustment of crowded units to their allotted space, may often be more properly regarded as geometrical rather than morphological, especially when any structural peculiarity is concerned (FIG. 1).

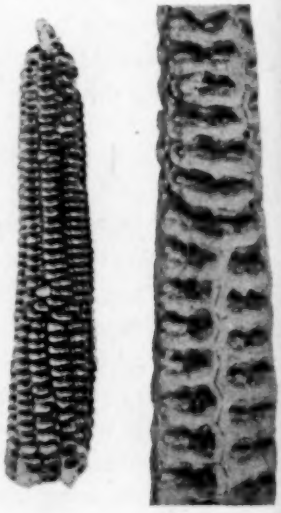

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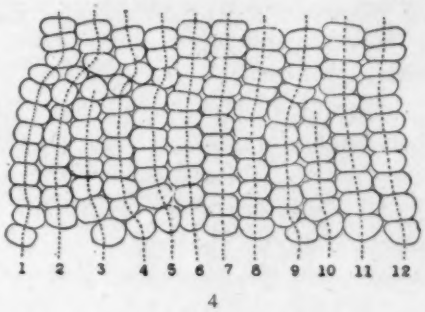
FIG. 2. An ear of corn with ten rows at the base and eight at the tip, × ½. FIG. 3. The cob of the ear shown in FIG. 2, after treatmentas described in the text, × 1⅛.

A reliable technique to bring out the arrangement of the spikelets, when any irregularity is evident, may be borrowed from the maker of corncob pipes. The first step in the process, after the removal of the kernels, is to shave off with a sharp knife the chaff on the outside of the cob.

This chaff consists of the glumes and palets of the spikelets, and its removal exposes the alveoli, in each of which a pair of spikelets is borne. When these alveoli are brought out clearly, the work may be finished with a piece of sandpaper, but this is usually unnecessary. Any corncob, typical or anomalous, when treated in this way, displays a number of longitudinal series of alveoli corresponding to the rows of paired spikelets.

The results secured when this method is applied to an ear having more rows at the base than at the tip are best explained by reference to the figures. Fig. 2 is an ear of flint corn with ten rows at the base and eight at the tip; four rows are seen apparently giving place to two near the middle of the ear. If this change occurs as Collins explains it, we should find on the cob of this ear five rows of alveoli running full length; but FIG. 3, which shows a portion of the cob of this ear treated as above described, shows the fallacy of this theory. There are five rows of alveoli at the base and four at the tip, the change in number occurring at the exact point where two rows of grains are dropped. These results were duplicated with several ears, no ear being found



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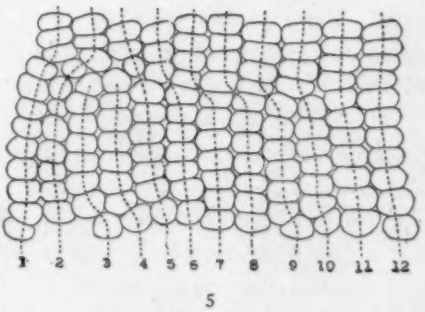

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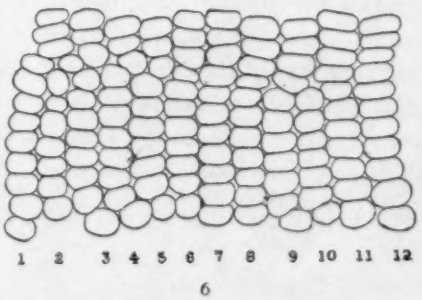

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FIG. 4. Transition from twelve to ten rows.
FIG. 5. The erroneous explanation of FIG. 4; the dotted lines indicate the continuity of rows.
FIG. 6. The correct explanation of the transition indicated in FIG. 4.

that gave contrary results; particularly striking results were obtained with an ear having ten rows at one end and eighteen at the other (FIG. 1). The evidence is conclusive that the difference in number of rows is due to the discontinuance of a row of pairs of spikelets and not to the abortion of the pedicelled spikelets of two such rows.

FIGS. 4–6 show, in a composite camera lucida drawing, a belt around an ear, covering the point of transition from twelve rows to ten. The structure of the ear shows that 1 and 2, 3 and 4, 5 and 6, etc., are respective pairs of rows. FIG. 5 shows Collins's interpretation of the loss of rows, if this is a case where the location of rows can be determined with what he calls "reasonable certainty" (p. 134); rows 3 and 10, representing the pedicelled spikelets of their respective pairs, are dropped. But the method here described removes all doubt and is applicable to all ears regardless of their external aspect. It shows, as in FIG. 6, that the two rows lost constitute one pair.

It is probably incorrect to speak of the "loss" of rows except as an event incident to our progress in examing the ear from one end to the other, for the actual *loss* of rows in this case is probably not a fact of either phylogeny or ontogeny. There is nothing to indicate that the short rows represent long rows partially aborted. In fact the abortion of spikelets or of rows in the ear seems to be much more constant as a characteristic of theories demanding it for consistency than of real ears of corn; and the integrity of the pair of pistillate spikelets seems to be maintained quite as constantly in maize as is the abortion of one of the pair in teosinte.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1919–1920

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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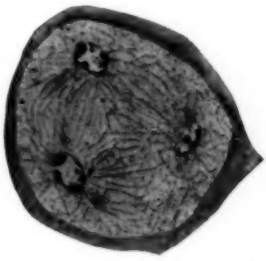

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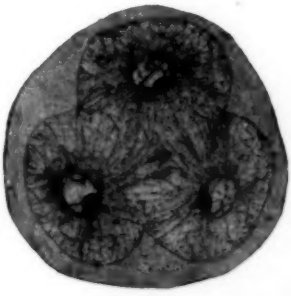

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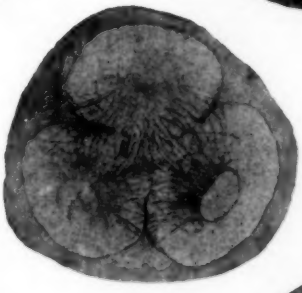

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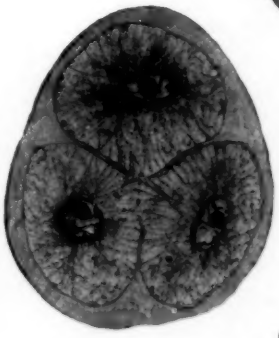

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